

Differential Selection for Vegetative Structure Between Juvenile Brown Shrimp (*Penaeus aztecus*) and White Shrimp (*P. setiferus*), and Implications in Predator–Prey Relationships

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The distributions of juvenile brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, (57–72 mm TL) were monitored in partially vegetated laboratory enclosures to examine selection for vegetative structure. Simulated *Spartina* culms, composed of green straws, were used as structure in the experiments. Brown shrimp selected for this structure during the day but not at night. White shrimp showed no strong selective preference for structure during the day or night.

Selection in the field was measured by examining densities of the two species of shrimp (40–80 mm TL) in a Galveston Bay, Texas, salt marsh. Brown shrimp were more abundant in vegetated habitats (*Spartina alterniflora*) than in adjacent non-vegetated areas. Differences in white shrimp densities between the two habitats were variable, and no consistent pattern was observed.

Laboratory predation experiments were conducted in non-vegetated and vegetated cages using Atlantic croaker (*Micropogonias undulatus*) as predators. In non-vegetated cages there was no significant selection for either species of shrimp by the fish. In partially and completely vegetated cages, fish selected white shrimp over brown shrimp. These data suggest that the presence of vegetation alters prey selection by Atlantic croaker, and this interaction may result in greater mortality of white shrimp compared with brown shrimp in salt marshes.

Introduction

Both brown shrimp, *Penaeus aztecus* Ives, and white shrimp, *P. setiferus* (Linnaeus), utilize estuaries as nursery grounds. Within estuaries, however, there is evidence that these species differ in selectivity for vegetated habitats. In Mobile Bay, Loesch (1965) reported that 15–70 mm (total length, TL) brown shrimp were concentrated in areas

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with submerged vegetation (*Ruppia* and *Vallisneria*), and white shrimp, of similar sizes, were prevalent in non-vegetated areas with large amounts of organic detritus. In the Laguna Madre, Texas, Stokes (1974) recorded white shrimp to be most abundant in non-vegetated areas while brown shrimp were collected on non-vegetated bottom and in seagrass beds. Although intertidal marsh vegetation is dominant in estuaries of the northwestern Gulf of Mexico, where brown shrimp and white shrimp are most abundant, field data on differences in selectivity for this vegetation have been limited due to sampling problems. In Galveston Bay, Texas, however, Zimmerman *et al.* (1984) and Zimmerman and Minello (1984) demonstrated that post-larval and juvenile brown shrimp were most abundant in habitats vegetated with *Spartina alterniflora* compared with adjacent non-vegetated areas. White shrimp were abundant in both vegetated and non-vegetated habitats. In laboratory experiments, using small aquaria, Giles and Zamora (1973) reported that both species, when present alone, selected for areas vegetated with *Spartina*. When the two species were mixed, however, there was an apparent displacement of white shrimp onto non-vegetated bottom.

Estuarine vegetation, mostly seagrasses, has been shown to reduce predator-related mortality on small fish (Lascara, 1981), bivalves (Peterson, 1982), and crustaceans (Nelson, 1979; Stoner, 1979; Coen *et al.*, 1981; Heck & Thoman, 1981). Vince *et al.* (1976) and Van Dolah (1978) also concluded that *Spartina* can offer amphipods and small gastropods protection from fish predators. Our laboratory results have shown that artificial vegetation, resembling *Spartina*, reduced predation rates on brown shrimp by some estuarine fish predators (Minello & Zimmerman, 1983).

Differences between brown and white shrimp in selection for vegetative cover may result in differences in predatory pressure on the two species. In this study we examined differences in selectivity for *Spartina* structure, and the effect of these differences on predation by a common estuarine fish predator, the Atlantic croaker, *Micropogonias undulatus* (Linnaeus).

Methods and materials

Shrimp and Atlantic croaker were collected from Galveston Bay, Texas with trawls and seines. Shrimp, fed pelleted food daily in holding tanks, were not fed during experiments. Atlantic croaker were fed a mixture of live brown shrimp and white shrimp for a minimum of 5 days, and were starved for 24 h before the predation experiments. All laboratory experiments except one were conducted during the summer of 1982. The selective predation experiment with no vegetation and a thin shell substrate was completed during the summer of 1983.

Experiments were conducted in circular cages (1.5 m diameter, 1 m high, 1.8 m² bottom area) placed in large concrete tanks. Tanks were located in a building with a white translucent roof, allowing the use of natural photoperiods. Salinities were maintained at 24–26‰, and temperatures varied between 27.5 and 30.7 °C. *Spartina* culms were simulated using green straws mounted in a plastic mesh at a density of 880 culms m⁻². Straws were arranged in evenly distributed clumps (18 straws per clump), with approximately 10.5 cm between clumps. Additional details are given in Minello and Zimmerman (1983).

Selection for vegetative structure in the laboratory

Selection for vegetative structure by shrimp was examined by using three cages in which straws covered 50% of the bottom. The substrate consisted of a thin layer of crushed

shell and sand. Shrimp could not burrow out of sight in this substrate. The distributions of shrimp (57–72 mm TL) within each cage were examined for each species separately (15 shrimp per cage) and both species combined (10 shrimp of each species per cage). Shrimp in the non-vegetated half of the cages were counted every 3 h for at least a 2-day period. The percentage of shrimp within the vegetation was inferred from these data. When both species of shrimp were present, loops of different coloured thread tied just anterior to the telson were used to identify species. Observations at night were made using a red light.

After 3 days of observations with both species of shrimp present, three Atlantic croaker (110–125 mm TL) were placed in each cage, to examine the effect of non-feeding fish on the distributions of the shrimp. The mouths of the fish were sewn partially closed, preventing them from feeding on shrimp. This procedure had no apparent effect on either the swimming behaviour of the fish, or the ability to move water over the gills. Observations on the distributions of both shrimp and fish were continued for an additional 2 days. Diel activity (swimming or stationary on bottom) patterns of the fish were also recorded.

Shrimp redistributed themselves frequently within the experimental cages, and the distributions of animals from one day to the next were considered to be independent. Our data on the distribution of shrimp for each of the eight time periods during a day, therefore, consisted of six to nine independent observations (three cages \times 2–3 days) of the percentage of shrimp in the vegetated half of the cage. Observed values were mostly between 30 and 70%, and the data were not transformed (Sokal & Rohlf, 1969). A *t*-test was used to determine whether the mean percentages differed significantly from the expected 50%. Chi-square analysis on pooled data gave similar results.

Predation experiments

Selective predation on brown and white shrimp was examined in the laboratory using Atlantic croaker as predators. Experiments in non-vegetated and half-vegetated cages were conducted with substrates similar to those used in the experiments on selection for structure by shrimp. Additional experiments were conducted in both non-vegetated and completely vegetated cages with a 40-mm layer of sand as substrate. Brown shrimp frequently burrowed out of sight during the day in this substrate. The two experiments with sand substrates were conducted concurrently.

In all experiments, three fish were placed in each of three replicate cages during the day, at least 6 h before introducing shrimp. Ten individuals of each species of shrimp were added to the cages after dark. Fish were allowed to feed for 24 h, tanks were drained, and the number of shrimp of each species remaining in the cages was recorded. Data were pooled from the three replicate cages, and a G-test was used to test for independence between mortality and prey species (Sokal & Rohlf, 1969).

Non-vegetated control cages, with 10 individuals of each species of shrimp but without fish, were used to examine mortality unrelated to predation during the experiments. Of the 60 shrimp in the controls, only one brown shrimp was not recovered alive.

*Selection for *Spartina alterniflora* habitat in the field*

Densities of shrimp (40–80 mm TL) were also examined in a Galveston Bay salt marsh, dominated by *Spartina alterniflora*, during eight sampling periods between 26 April and 8 December, 1982. During each sampling period (3-day duration), 12 pairs of samples were collected using a 2.8 m² drop sampler. Each pair consisted of one sample in a

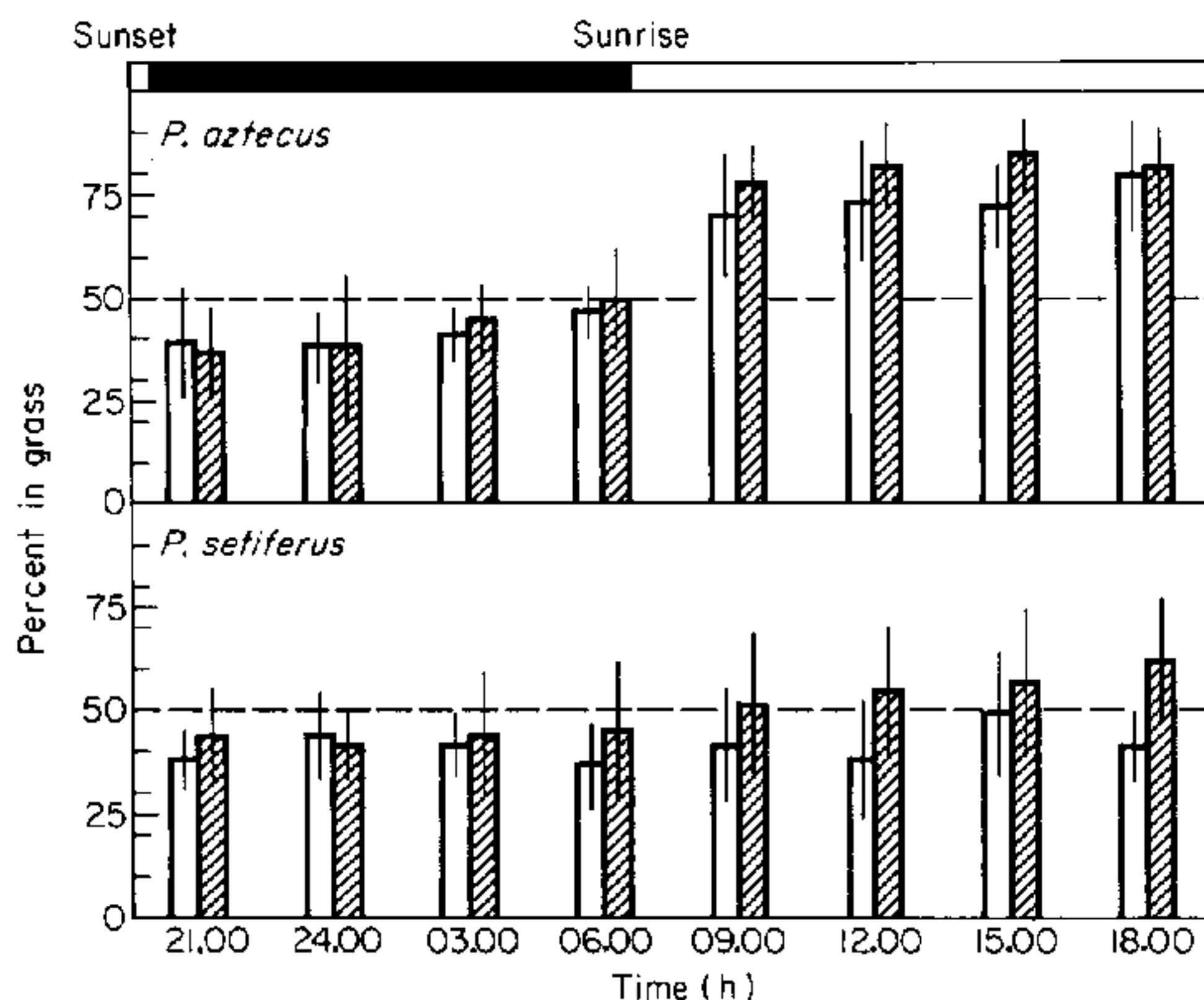


Figure 1. Selection by shrimp for vegetative structure. Histograms represent mean percentages ($n=6-9$) of shrimp in the grass during each time period (15 shrimp per observation when species were separate; 10 shrimp per observation when species were combined). Vertical lines are 95% confidence intervals (untransformed data). □, Species separate; ▨, species combined.

vegetated area and one sample in an adjacent non-vegetated area. All samples were collected during the day at high tide. Densities of brown and white shrimp in both habitats were recorded, and a sign-rank test (Tate & Clelland, 1957) was performed to determine whether selectivity for either habitat was significant. Details of the sampling methods plus additional data have been reported by Zimmerman *et al.* (1984) and Zimmerman and Minello (1984).

Results

Selection for vegetative structure in the laboratory

When species were examined separately, brown shrimp selected strongly for vegetative structure during daylight hours with mean percentages in the grass ranging from 70 to 80% (Figure 1). There appeared to be a selection for non-vegetated bottom during the night, though it was less intense and was significant for only two of four nighttime periods. Mean percentages of white shrimp in the grass were never more than 50%, and selection for vegetation was not apparent. Selection for non-vegetated bottom, however, occurred during the night.

When both species were present in the cages, a similar pattern of day-night distribution was apparent (Figure 1). Brown shrimp selected strongly for the vegetated half of the cages during the day, but the mean percentage of white shrimp in the grass was never significantly above 50%. Overall, the percentages in the grass of both species were higher than the values obtained for species tested separately. A comparison of mean percentages for each time period, however, indicated no significant differences.

The presence of non-feeding predators (Atlantic croaker with their mouths sewn closed) in the cages did not significantly alter the distributions of the shrimp (Figure 2). Mean percentages in the vegetated half of the cages, however, for brown and white shrimp, were reduced during the day. This reduction coincided with movement of the

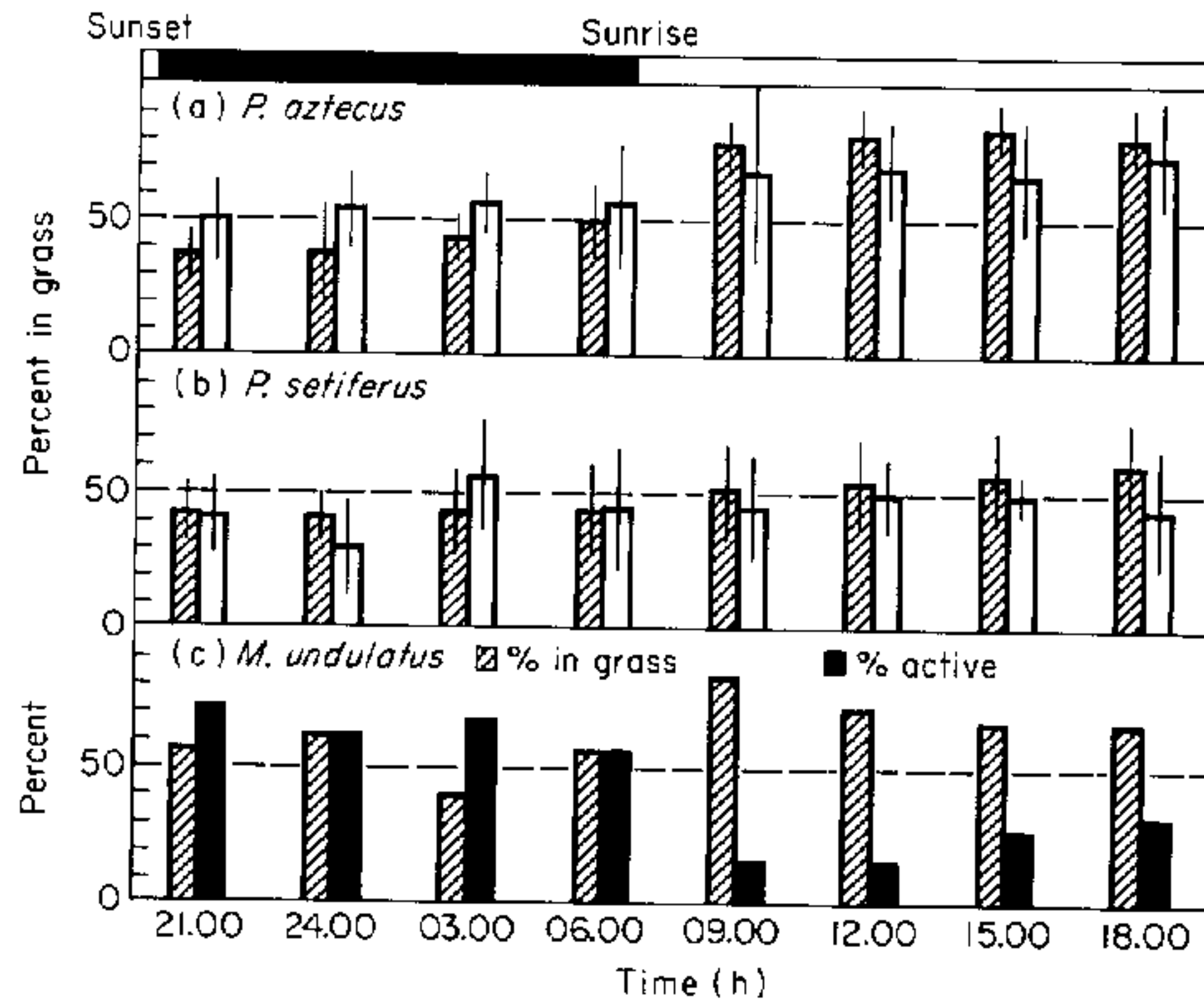


Figure 2. The effect of potential fish predators (Atlantic croaker) on selection of shrimp for vegetative structure. Histograms represent mean percentages of (a) brown and (b) white shrimp in the grass (both species present: \square , with predators; ▨ , without predators). The percentage of Atlantic croaker in the grass and the diel activity pattern of the fish are shown in (c).

fish into the vegetation during daylight hours (Figure 2). The mean percentages of brown shrimp in the grass increased at night when predators were present. The fish were most active at night, frequently moving in and out of the vegetated areas.

In all of these experiments, brown shrimp showed a selection for vegetative structure during the day. In addition, in the presence of fish, mean percentages of brown shrimp in the grass were above 50% for seven out of the eight time periods examined (only two means were significantly above 50% at the 0.05 level). The overall distributions of white shrimp indicated that this species did not select for vegetative structure under our experimental conditions.

Predation experiments

In non-vegetated cages with either thin shell or sand substrates, results varied among replicates (Table 1), but overall, Atlantic croaker did not select for either white or brown shrimp. In the half-vegetated cages, Atlantic croaker selectively preyed upon white shrimp rather than brown (Table 1). This selection was consistent in the three replicate cages, and the G-test was highly significant ($P < 0.005$). In completely vegetated cages with a sand substrate, there also was a consistent selection for white shrimp over brown by the fish (Table 1). The G-test for the pooled data was marginally significant ($P = 0.025-0.050$), indicating that mortality was not independent of the prey species.

The results of G-tests strongly suggest that Atlantic croaker select for white shrimp in the presence of vegetative structure and show little prey preference in the absence of vegetation. However, a direct test of the effect of vegetation on prey selection, using mean percentages of white shrimp eaten out of the total number of shrimp eaten in the six cages with thin shell substrates, was not significant (t -test, $P > 0.20$, $n = 3$). The variability among cages was relatively high, and this lack of significance could be due to the low power of the test with only three replicates per treatment.

The possibility of size-selective predation by the fish interacting with selection for shrimp species was examined by comparing size-frequencies of shrimp used in the

TABLE 1. Selective predation on brown and white shrimp by Atlantic croaker

	Predator size (mm TL)	Prey size (mm)	Cage	Number of shrimp available (50% brown, 50% white)	Number of shrimp eaten	Number of white shrimp eaten (% of total eaten)	P^a (G-test)
Half-vegetated cages with thin shell substrate	137-163	55-70	1	20	15	9 (60)	<0.005
			2	20	8	7 (88)	
			3	20	9	6 (67)	
			Σ	60	32	22 (69)	
Non-vegetated cages with thin shell substrate	136-172	60-70	1	20	16	7 (44)	>0.20
			2	20	8	5 (63)	
			3	20	9	6 (67)	
			Σ	60	33	18 (55)	
Non-vegetated cages with sand substrate	117-127	57-70	1	20	9	7 (78)	>0.20
			2	20	10	4 (40)	
			3	20	12	6 (50)	
			Σ	60	31	17 (55)	
Completely vegetated cages with sand substrate	116-128	57-70	1	20	10	6 (60)	0.025-0.050
			2	20	7	5 (71)	
			3	20	9	6 (67)	
			Σ	60	26	17 (65)	

^a P = probability of independence between mortality and prey species.

experiments. Kolmogorov-Smirnov two-sample tests (Tate & Clelland, 1957) indicated no significant differences (0.05 level) either in the size-frequency distributions of brown shrimp and white shrimp available to the predators or in the size-frequency distributions of shrimp eaten *vs.* those not eaten.

Selection for Spartina alterniflora habitat in the field

Densities of brown and white shrimp of all sizes in vegetated and non-vegetated habitats have been reported by Zimmerman *et al.* (1984) and Zimmerman and Minello (1984). Only the data on 40-80 mm (TL) shrimp are reported here since these sizes are comparable to the sizes of shrimp used in the laboratory experiments. Shrimp in this size range made up a relatively small percentage (10-16%) of the total number of shrimp collected in the marsh.

Mean densities of brown shrimp in *Spartina* ranged from 0.9 to 25.9 shrimp per 10 m² over the eight sampling periods (Table 2). In non-vegetated habitat, densities ranged from 0 to 6.3 shrimp per 10 m². During each sampling period, mean densities were always higher in the vegetation, and the sign-rank tests indicated a significant preference for the vegetated habitat during six of these periods (Table 2). The test could not be performed on the data from two of the sampling periods because the number of non-zero comparisons was too small.

Mean densities of white shrimp ranged from 0 to 54.0 shrimp per 10 m² in the vegetation and 0 to 19.3 shrimp per 10 m² in the non-vegetated habitat. The sign-rank test could be performed on the data from only four of the sampling periods. Selection for vegetated habitat was apparent during August and November (Table 2). In October, however, there was a highly significant selection for non-vegetated habitat, and in

TABLE 2. Differences in habitat selection between brown (*Penaeus aztecus*) and white (*P. setiferus*) shrimp (40–80 mm) in a Galveston Bay salt marsh. Selection for areas vegetated with *Spartina alterniflora* (VEG) or adjacent non-vegetated habitat (NVEG) was determined using a sign-rank test on densities from 12 pairs of samples collected during each sampling period

Sampling period	<i>P. aztecus</i>		<i>P. setiferus</i>	
	Selection	Mean density ^a (10 m ⁻²) VEG/NVEG	Selection	Mean density ^a (10 m ⁻²) VEG/NVEG
26–28 Apr	VEG**	25.0/6.3	No test	0/0
26–28 May	VEG**	25.9/6.3	No test	0/0
22–24 Jun	VEG**	25.3/1.5	No test	2.1/1.2
21–23 Jul	No test	0.9/0.3	No test	0.9/0.3
30 Aug–1 Sept	VEG**	5.1/0	VEG**	11.0/0
13–15 Oct	VEG*	6.0/0.9	NVEG**	1.8/13.7
8–10 Nov	VEG*	4.8/0.3	VEG*	54.0/19.3
6–8 Dec	No test	0.9/0.6	N.S.	17.3/9.2

^a*n* = 12; ***P* < 0.01; **P* = 0.05–0.01; N.S., *P* > 0.20.

December densities were relatively high in both habitats, with no significant selection apparent.

Discussion

Our laboratory and field data appear consistent with the hypothesis that brown shrimp select for vegetated habitats more frequently than white shrimp. The data from a Galveston Bay salt marsh show a consistent pattern during the day of higher densities of brown shrimp within areas vegetated by *Spartina alterniflora* compared with adjacent non-vegetated habitats. The density differences between the two habitats were more variable for white shrimp. These data agree with the distributions of these two species reported by Loesch (1965) and Stokes (1974) in other estuarine areas.

Field densities do not necessarily indicate active selection for a habitat. Differences in habitat-specific mortality may also be involved. Our laboratory work suggests, however, that an active selection component is responsible for the observed field distributions of shrimp in salt marshes. In half-vegetated cages, brown shrimp selected for vegetative structure during the day, while there was no such selection by white shrimp. Neither species selected for structure at night. The selection by brown shrimp for artificial vegetation in these experiments also indicates that attraction to vegetation, at least in part, is a direct response to the presence of structure.

Our laboratory results do not entirely agree with the data reported by Giles and Zamora (1973). In their study, brown and white shrimp, when present alone, apparently selected for vegetation during both day and night. In addition, there appeared to be a displacement of white shrimp onto non-vegetated bottom when the two species were combined. An examination of the major differences between these two studies (Table 3) suggests a number of factors that could be responsible for the disparity in results. The use of live *Spartina* with its epiphytic associates may have increased attraction to

TABLE 3. A comparative summary of data from the present study and the data reported by Giles and Zamora (1973)

	Giles and Zamora (1973)		Present study	
	Day	Night	Day	Night
<i>Results (% in grass)</i>				
Species separate				
Brown shrimp	86%	75%	74%	41%
White shrimp	80%	61%	42%	40%
Species combined				
Brown shrimp	88%	71%	81%	42%
White shrimp	41%	27%	56%	33%
<i>Methods and materials</i>				
Food	Present		Absent	
Container size	0.22 m ²		1.8 m ²	
Vegetation	Live <i>Spartina</i>		Artificial vegetation	
Shrimp size (total length)	51–70 mm		57–72 mm	
Shrimp densities				
Species separate	27 m ⁻²		8 m ⁻²	
	(6 per container)		(15 per container)	
Species combined	54 m ⁻²		11 m ⁻²	
	(12 per container)		(20 per container)	

vegetation in their study. Densities of shrimp in their aquaria were also higher than the densities used in our experiments and higher than any densities of 40–80 mm shrimp collected in a Galveston Bay salt marsh in 1982. The maximum density of shrimp of this size was collected in November within vegetation (17.5 white shrimp per m²). The relatively high densities used in their experiments (27–54 m⁻²) may be especially important in explaining the apparent interspecific interactions reported in their study.

Giles and Zamora (1973) also may have excessively inflated the number of observations used in their statistical tests by considering closely spaced (15–30 min) observations to be independent. Although this may not affect their conclusions, the validity of this technique is dependent upon the activity and movement of the shrimp within the experimental containers. As a result, actual probability levels of their chi-square tests may be considerably lower than those reported.

The presence of estuarine vegetation such as seagrasses and algae appears to reduce predation on some organisms (Nelson, 1979; Stoner, 1979; Coen *et al.*, 1981; Heck & Thoman, 1981; Lascara, 1981; Peterson, 1982). *Spartina* apparently functions in a similar manner (Vince *et al.*, 1976; Van Dolah, 1978), and the presence of artificial *Spartina* has been shown to reduce predation on juvenile brown shrimp by pinfish (*Lagodon rhomboides*) and Atlantic croaker (Minello & Zimmerman, 1983). Differences in selectivity for vegetation between brown and white shrimp, therefore, may result in differences in predation on these species.

Data from our predation experiments suggest that white shrimp are more susceptible to predation by Atlantic croaker than brown shrimp in the presence of vegetative structure. In half-vegetated cages, there was a strong selection by Atlantic croaker for white shrimp, and differences between the two prey species in selectivity for the vegetated half of the cages may have been partially responsible. Selective predation was not exhibited in the absence of vegetation. The presence of a sand substrate in one of the non-

vegetated experiments introduced possible species differences in burrowing behavior as a factor. Wickham and Minkler (1975) found that white shrimp did not burrow in a shell-sand substrate, but that brown shrimp burrowed during the day. Our unpublished laboratory results indicate that white shrimp (30–40 mm) will burrow during the day in sand substrates. Brown shrimp, however, burrow deeper and more frequently. Williams (1958) reported similar differences between the two species. If differences in burrowing habits offer selective protection from fish predation, white shrimp should be more susceptible to predation in cages with a sand substrate. The overall lack of selection for white shrimp over brown shrimp by Atlantic croaker in the non-vegetated cages with sand substrates, therefore, strengthens our conclusion that these predators do not select for either prey species in the absence of vegetation.

We can only speculate as to the reasons for the marginally significant selection for white shrimp by Atlantic croaker in the completely vegetated cages with a sand substrate. Differences in the protective nature of vegetative structure for the two species may be involved. Structure may not offer white shrimp protection from Atlantic croaker. There may also be an interaction between the burrowing behaviour of the two species and the presence of vegetation that could affect selective predation. The overall results of our predation experiments, however, suggest that the presence of vegetative structure alters prey selection by Atlantic croaker, increasing the proportion of white shrimp in their diet. This could result in greater mortality of white shrimp compared with brown shrimp in estuarine systems dominated by vegetation.

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